THE VERTICAL MIGRATION OF THE COPEPOD ACARTIA TONSA UNDER CONTROLLED ILLUMINATION

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Introduction

Vast numbers of plankton organisms are known to rise toward the surface of the water at night and sink downward during the day. This vertical migration was first studied by the great oceanic expeditions of the last century, particularly that of the "Challenger" in 1872 (Murray and Hjort, 1912). The first laboratory investigations were those of Groom and Loeb (1890) and Parker (1902). The earlier work has been extensively reviewed by Russell (1927) and Kikuchi (1930).

It was soon apparent that light was the main environmental factor involved, but many diverse conclusions were made as to its mode of action. These may be summarized as follows:

(1) *Phototropism overcoming geotropism.*—Parker (1902) found that *Labidocera aestiva* rose at night because of its negative geotropism, but sank during the day because this was overcome by its negative phototropism.

(2) *Light changing the sign of geotropism.*—*Cyclops albidus* was found to be geopositive in the light and geonegative in the dark (Esterly, 1907). Field observations on *Cyclops* by Worthington (1931) and Southern and Gardiner (1932) support this view.

(3) *Optimum light intensity.*—Rose (1925) placed various copepods in a horizontal tube with a graded light intensity, and found that the animals gathered in an intermediate zone. Field observations indicate that *Calanus* (Russell, 1926, 1928, 1934), *Metridia* (Clarke, 1933, 1934) and other forms follow a zone of optimum intensity.

(4) *Relative optimum intensity.*—*Daphnia* was found by Clarke (1930) to have a "primary" negative phototropism, which is strengthened by an increase of light intensity. When the intensity is reduced, the animal acquires a "secondary" positive phototropism and moves toward the light as long as it is being reduced. But if the intensity is held constant, the primary sign returns, and the animal moves away from the light. There is only a relative optimum here, the animal becoming adapted to the intensity existing at the moment. Such a mechanism is suggested by field observations of *Acartia clausi* (Johnson, 1938).

Other experiments have led to diverse conclusions. Johnson and Raymont (1939) found that *Centropages typicus* moved towards the light when the intensity is either increased or decreased. Downward movements during the night, when light intensity is constant, have been reported by several field workers (e.g., Waterman et al., 1939). These authors suggest that light merely keeps in phase internal physiological cycles which regulate the migration of the organisms. Esterly (1917*b*) found that *Acartia tonsa* kept in constant darkness moved upward on two successive evenings, suggesting the influence of an internal rhythm.

In none of these studies has vertical migration actually been reproduced. Groom and Loeb (1890) watched *Balanus* nauplii performing their diurnal migrations in a glass of water on the window, while Parker (1902) noted the migration of *Labidocera* in a floating jar outside the laboratory. But aside from these early observations, there are no reports of diurnal migrations being performed under controlled conditions. Many of the conflicting results may have been caused by subjecting the animals to laboratory situations which would never be encountered in nature. Thus Loeb (1908) concluded that vertical migration is caused by the difference in temperature between warm waters near the surface and cool deep waters. This obviously cannot apply to migration in those lakes where no temperature gradient occurs (Worthington, 1931). The observation of Clarke (1930) that the phototropic sign of *Daphnia* is reversed by changing light intensity, cannot apply to the downward migration of this form beginning at midnight (Southern and Gardiner, 1932). It was therefore decided to inquire if vertical migration could be reproduced under conditions approximating natural ones as closely as is possible in the laboratory. If so, it would then be possible to alter various factors in order to find the controlling ones.

Apparatus and Procedure

Animals collected by towing an open net were brought into the laboratory and placed in tall glass cylinders exposed to window light. The cylinders were placed in a large tank filled with water to permit control of the temperature. Observations were made by removing the cylinders from the tank and noting the vertical distribution of the animals.

Specimens of the copepod *Acartia tonsa* Dana were obtained by towing an open net for five minutes at a depth of 3 meters at the head of Woods Hole Harbor. The animals were collected in a small bottle towed at the end of the net; to avoid overcrowding they were transferred to a larger bottle as soon as the net was hauled aboard. The catch was

immediately brought into the laboratory and poured into finger bowls. Individual *Acartia tonsa* were identified under a dissecting microscope, picked up in a pipette, and placed 20 each in six glass cylinders, 48.5 × 4.5 cm., filled with sea water to a height of 43–44 cm. The cylinders were placed in a black-walled tank, 46 × 66 × 45 cm., open at the top, and placed in front of a window. The tank was filled to the water line in the cylinders with fresh water, which was kept at 15° by a thermostat attached to a refrigerating unit. Surface temperature in the harbor at the time of the hauls was 18–21° C.

The animals were fed with the diatom *Nitzschia closterium,* found by Clarke and Gellis (1935) to be a favorable diet for copepods. The diatoms were cultured by the method of Ketchum and Redfield (1938). A few drops of this culture were added to each cylinder every morning. Varying the time of feeding did not affect the behavior of the copepods.

Observations were made by counting the number of animals swimming in each vertical third of each cylinder. Since it was not possible to see animals lying on the bottoms of the cylinders, they were computed by subtracting the total number of animals swimming at any count from the highest total obtained in subsequent counts in that cylinder during the day. Thus, if six animals were observed swimming in cylinder II at 8:00 A.M., while ten animals were found swimming in the highest subsequent count of the day, it was assumed that four animals were resting on the bottom at 8:00 A.M. Dead animals are thereby eliminated, since they appear in no subsequent count of animals swimming. From this data, the percentage of animals in the top third of the cylinders was computed for each observation.

The cylinder to be counted was taken out of the tank and placed on a nearby shelf. Observations in the darkroom were made by turning on a 25-watt red lamp for one to two minutes while the animals were counted. This brief exposure to light did not affect their relative position. The remaining cylinders were covered during this time. The chief source of error in this procedure lies in the necessity of removing the cylinders from the tank for counting. Any such error is probably constant under the same light conditions, but may affect the results when different conditions are being compared.

Observations

Normal Behavior

The cylinders were first placed in front of an unobstructed south window, so arranged that they were never exposed to direct sunlight. Photometric observations showed that the light reaching the tank was

of approximately the same intensity as that at a depth of 10–20 meters in Woods Hole Harbor (Oster and Clarke, 1935). Normal vertical migration was carried on under these conditions for at least eight successive days. The animals moved up rapidly immediately following sunset, and then more slowly. The downward movement commenced at midnight, and proceeded slowly until dawn, when it became more rapid. The daytime level remained relatively constant (Fig. 1). The only field observations of the diurnal movements of *A. tonsa* are those made at La Jolla, California, by Esterly (1928). When the two curves

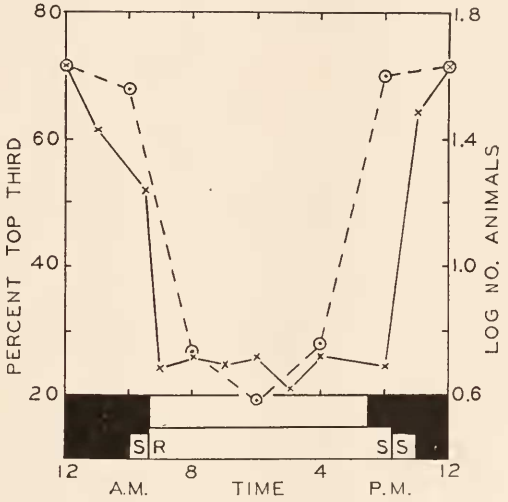

FIG. 1. Vertical distribution of *Acartia tonsa* in laboratory (solid line). Ordinate, percentage of animals in top third of cylinders; abscissa, time of day. Distribution in field (dotted line) from Esterly, 1928. Ordinate, mean logarithm of number of animals per haul; abscissa, time of day. *SR* represents sunrise, *SS* sunset. Upper bar for La Jolla, lower for Woods Hole. The shorter day in California seems to be correlated with a shorter downward movement.

are superimposed, the similarity of their shape indicates that the laboratory behavior is representative of that in the field.

An attempt was made to reproduce this behavior under more carefully controlled conditions. Room light was excluded by placing a tarpaper shelter over the tank. The cylinders were illuminated with daylight fluorescent lamps, chosen because their spectral energy distribution is approximately the same as that of daylight (General Electric Co., 1939). An opal glass diffusion screen was placed over these lamps to imitate the broad source area of window light. Four 24″ lamps were used, covered with a 14 × 24″ opal screen. To reproduce the

angle at which window light entered, the lamps were placed 60 cm. above the tank and 80 cm. to the side. The light now entered the cylinders at an average angle of 36° from the horizontal. Normal vertical migration continues under these conditions. The animals stay at the bottom of the cylinders during the day when the lights are on, and rise to the top at night when the lights are off (Table I).

TABLE I

Fluorescent light. Average of 60 A. tonsa at 15° C. for 48 hours; July 28–30, 1941. Observations in darkness are italicized.

Time	Percentage of Animals in Top Third of Cylinders	Time	Percentage of Animals in Top Third of Cylinders
6 A.M.	*52.2*	6 P.M.	9.55
8	13.4	8	7.97
10	3.50	10	*62.2*
2 P.M.	9.45	12 Midnight	*52.1*

Diurnal Rhythms

If this vertical migration is controlled by an internal rhythm, the normal movements should continue in constant darkness. Although the animals began their normal descent on the first morning of darkness, they did not leave the upper portion of the cylinders (Fig. 2). While no migration appears under these conditions, the normal behavior may be controlled by the coincidence of light and an internal rhythm set for the normal alteration of night and day. That this is not so is seen by the fact that the migration can be reversed by illuminating the animals at night and keeping them in the dark by day (Table II). It is significant, however, that the upward movement during the first reversed day is appreciably less than during the second. This behavior, together

TABLE II

Reversed day and night. Average of 120 A. tonsa at 15° C.
Observations in darkness are italicized.
July 31–August 1, 1941: Normal fluorescent light.
August 1–4: Reversed day and night.

Date	Percentage of Animals in Top Third of Cylinders					
	2 A.M.	8 A.M.	10 A.M.	2 P.M.	8 P.M.	10 P.M.
July 31					10.5	*51.1*
Aug. 1		*61.6*	0.81	21.6	10.8	14.3
2		14.3	*37.1*	*44.1*	*42.5*	12.1
3	18.2	15.2	*62.6*	*51.8*	*64.3*	*51.8*
4		*33.4*				

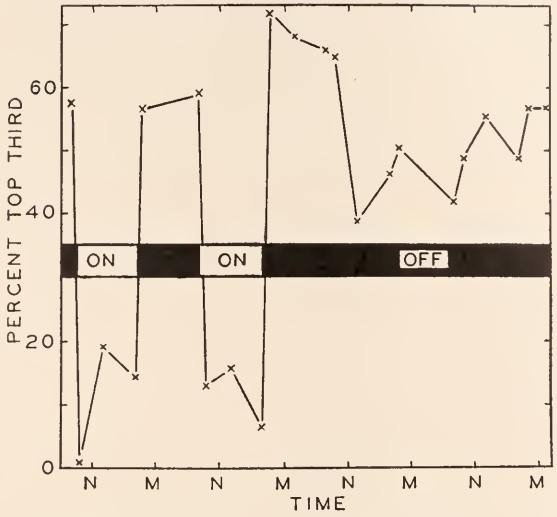

FIG. 2. Vertical distribution of *A. tonsa* in daylight fluorescent light and in constant darkness. Ordinate, percentage of animals in top third of cylinders; abscissa, time of day. *N* = noon; *M*, midnight.

with the downward movement during the first morning of constant darkness, indicates that traces of a metabolic rhythm, once set up, persist under changed conditions for one day. Although light alone seems to control the behavior of the animals under these conditions, it is possible that it is effective only if it operates in a 24-hour cycle. This is not so, however, since a 4-hour "day" can be induced (Table III).

TABLE III

Four-hour day. Average of 120 A. tonsa at 15° C.; August 4, 1941—fluorescent light. Observations in darkness are italicized.

Time	Percentage of Animals in Top Third of Cylinders	Time	Percentage of Animals in Top Third of Cylinders
10 A.M.	0.40	1:00 P.M.	*40.0*
11	*28.0*	1:15	0.40
12 Noon	*48.0*		

Changes in Illumination

The lighting conditions were now altered in order to find the specific factors controlling the migration of *A. tonsa*. No difference in behavior appeared when the opal glass screen was removed, showing that the area of the light source was of no significance (cf. Fig. 2: the first day is without the screen, the second with it). Spectral energy distribution

was found not to be a controlling factor, since incandescent bulbs were substituted for fluorescent lamps without effect. Bulbs of 25, 60 and 300 watts were used without changing the normal behavior, showing that light intensity within this range is not a factor in migration (Fig. 4).

An entirely different situation prevailed when the lamps were moved directly above the tank. Migration was now reversed, the animals mov-

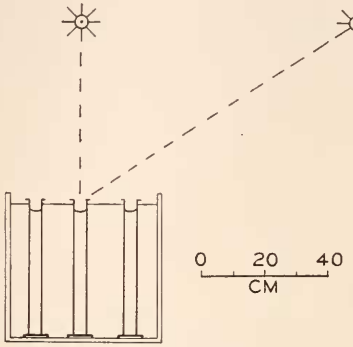

FIG. 3. Arrangement of oblique and overhead lights. Distances in centimeters.

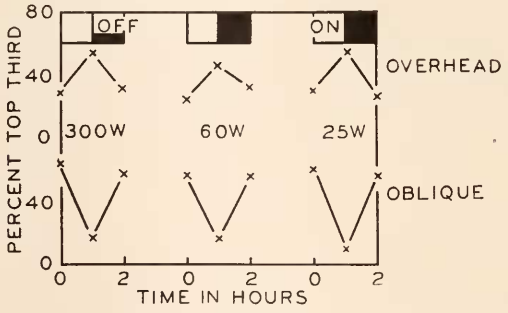

FIG. 4. Vertical distribution of *A. tonsa* in incandescent light. Top, lamps 60 cm. above tank; bottom, same, but 80 cm. to side. Ordinate, percentage of animals in top third of cylinders; abscissa, time in hours.

ing up in the light and down in the dark (Fig. 4). If the overhead lights are kept on for 24 hours, the copepods stay up throughout this period, although animals in oblique light for 24 hours stay down (Fig. 5). The animals move *up* in overhead light, or in darkness following oblique light; they move *down* in oblique light, or in darkness following overhead light. The downward movement when the overhead light is turned off lasts for only an hour. After this time the normal upward movement in darkness begins (Fig. 6). This upward movement con-

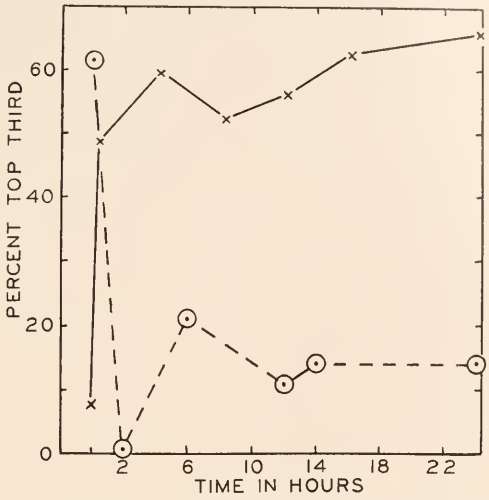

FIG. 5. Vertical distribution of *A. tonsa* in daylight fluorescent light. Solid line, lamps 60 cm. above tank; dotted line, same, but 80 cm. to side. Ordinate, percentage of animals in top third of cylinders; abscissa, time in hours.

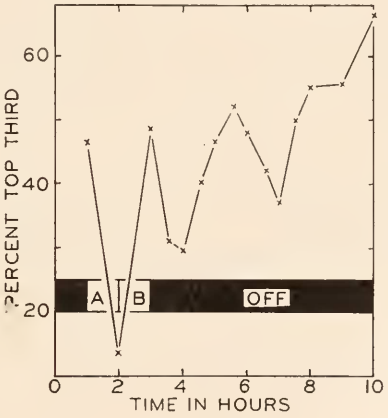

FIG. 6. Vertical distribution of *A. tonsa* under various light conditions. Ordinate, percentage of animals in top third of cylinders; abscissa, time in hours. *A*, Daylight fluorescent oblique; *B*, 25-watt overhead.

tinues for 1½ hours, to be followed by another downward movement, which in turn is followed in 1½ hours by an upward movement. If the animals have been kept up for 12 hours with overhead light, they will stay down in the dark for the next 12 hours.

A simple but dramatic presentation of these results can be made by leaving a cylinder containing *A. tonsa* in the dark for an hour. If a

weak red light is now turned on for a few moments, the animals may be seen slowly swimming about, the greater number at the top of the cylinder. If a white light, level with the center of the cylinder but several feet away, is now turned on, a remarkable change occurs in the behavior of the animals. First one and then another stops swimming and sinks slowly downward, head up, antennae outspread. Occasionally an individual swims about for a moment, but it soon stops and continues sinking downward. In ten minutes almost all the animals will be at the bottom of the cylinder. If the light is now placed on top of the tube, the animals swim rapidly upward. Some individuals, seemingly unable to get close enough to the light, hurl themselves time after time against the surface of the water.

Movements of Individuals

It has hitherto been impossible to determine whether vertical migration consists of mass movements of entire populations, or of a general trend of diverse individual movements. Thus Fig. 1 shows that about 20 per cent of the animals are on the surface during the day, and 70 per cent at night. Does this mean that only 50 per cent of the animals actually migrate, or that all the animals spend 20 per cent of their time on the surface during the day, and 70 per cent at night? To answer this question, 42 individuals were tested in oblique light, in overhead light,

TABLE IV

Individual movements of 42 A. tonsa *at 15° C.;* August 18–23, 1941.

Light Conditions	Time	Animals in Top Third of Cylinders	Average Movement of 42 Individuals*
	hours	*per cent*	
Dark	1	60.0	
	2	58.4	1.9
	3	77.8	1.8
	4	63.8	1.5
Fluorescent Oblique	5	23.3	2.0
	6	23.3	2.2
	7	27.8	1.6
	8	27.8	1.6
Dark	9	63.4	1.6
	10	66.6	1.9
	11	58.3	1.7
	12	79.2	1.2
25w Overhead	13	72.2	1.1
	14	58.3	1.2

* Each unit represents one-sixth of cylinder, or 7 to 7.5 cm.

and in the dark. The cylinders were divided into sixths numbered from top to bottom. The average distance moved per hour was measured in units representing one-sixth of a cylinder (Table IV, Fig. 7*A*). The average behavior of the entire group gives the same results as before, but the individuals are seen to be continually moving. Each animal traverses about one-third of a cylinder (14–15 cm.) every hour. Maximum movement occurs two hours after the lighting is changed. Too

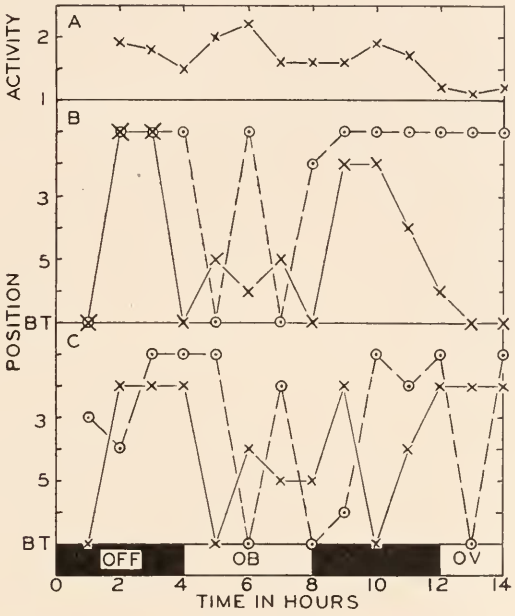

Fig. 7. *A*, average movements of 42 individuals. Ordinate, activity in units representing one-sixth of a cylinder; abscissa, time in hours. *B*, Positions of two males. *C*, Positions of 2 females. Ordinate, position of animals in sixths of cylinders, numbered from top to bottom; abscissa, time in hours; *Bt* indicates resting on bottom; *OB* indicates daylight fluorescent, oblique; *OV*, 25-watt, overhead.

few males were present to permit a statistical comparison of the sexes, but no significant differences are found between the records of individual males and females (Fig. 7). Because of the greater distances covered, the proportion of these scattered movements to the entire migration may not be as great in nature as in the laboratory. These diverse movements suggest why field observations do not show that all of the animals are right on the surface at night, and down on the bottom during the day.

Discussion

It might appear that the difference between the behavior of the animals in overhead and in oblique light is caused by the intensity of the light, since the lamp is closer to the cylinders in the overhead than in the oblique position. But measurements of light intensity show that this factor must be eliminated, since the intensities of the various sources of oblique and overhead light overlap (Table V). The only remaining difference is in the positions of the lamps.

Table V

Light intensity measured by "Photox" cell with ½" diaphragm.

Light Source	Position of Bulb	
	Oblique	Overhead
Window	2.8 m.a.	
Incandescent bulb		
25-watt	0.8	1.7 m.a.
60-watt	1.5	3.8
300-watt	5.2	14.0
Fluorescent lamps		
with screen	1.0	
without	2.5	

It is believed that the control of this behavior lies in the directional character of the illumination. The overhead light appeared to shine directly down the cylinders with little deflection. The oblique light, on the other hand, entering at an average angle of 36° from the horizontal, appeared to be reflected from the walls of the tank and cylinders so as to provide a more diffuse illumination (Fig. 3). Additional evidence is provided by tropism experiments in a horizontal glass trough. This trough, which could be illuminated by an incandescent bulb at either end, was surrounded by water to minimize reflection from the side. Under this highly directional illumination, *A. tonsa* always moved toward the light. By turning on first the lamp at one end and then that at the other, it was possible to keep an individual moving back and forth from end to end indefinitely. But the distribution of light in natural waters, according to recent measurements, does not show this highly concentrated character. Whitney (1941) found that the light intensity at a depth of 3 meters in Woods Hole Harbor was distributed as follows:

overhead 12 units
towards sun 16 units
horizontally 2 units
from below 1 unit

Although similar measurements could not be made in the cylinders, the oblique light appeared to provide a comparable situation. Overhead light, or the light in the horizontal trough, seemed to be of a much more concentrated character. It is believed that this difference in the concentration of the light is the only factor that can account for the difference in behavior.

This view is supported by several reports in the literature of animals which are positive to direct light, but which move down in diffuse light and up in the dark. Such behavior has been found in the larva of *Corethra plumicornis* (Harper, 1907), in *Branchipus serratus* (McGinnis, 1911), *Daphnia pulex* (Dice, 1914), and *Sagitta bipunctata* (Esterly, 1919). Two of these three relations have been described for *Cyclops albidus* (Esterly, 1907), for the nauplii of *Balanus perforatus* (Ewald, 1912), for *Paramoecium* and the larvae of the echinoid *Diadema setosum* (Fox, 1925), and for six Crustacea (Kikuchi, 1938).

In diffuse light, all parts of the photoreceptor will receive illumination of equal intensity. In direct light, on the other hand, that part of the receptor facing the source will be strongly illuminated, while much less light will come from the side. There is no need for the light to be perfectly direct or diffuse, since a threshold ratio of front light to side light may determine the behavior.

We may then conclude that:

(1) *Acartia tonsa* sinks downward in light which is not highly directional. This behavior, together with its upward movement in darkness, is believed to account for the normal vertical migration of this form.

(2) *A. tonsa* moves toward a source of highly directional light. Such illumination is not likely to be encountered in nature.

This theory will explain the paradox of an animal which moves toward the light in the laboratory, but away from it in the field. It seems to account for the fact that positively phototropic plankton do not come to the surface of the sea during the day, and also, that positively phototropic insects do not fly up to the sun.

If light alone controls the movements of these animals, we could not account for the oscillating movements in darkness following overhead light (Fig. 6). The movement toward the light, however, may result in fatigue, and the animal will then sink down. On recovery, the animal swims up, to sink down again when fatigued. Such oscillations may explain downward movements beginning at midnight, reported from both field and laboratory (Fig. 1), as well as the upward movements in constant darkness observed by Esterly (1917*b*).

There is no justification for applying the results of these experiments to vertical migration in general. Thus, while *Acartia tonsa* continues its response to light for at least 48 hours, another species of the same genus, *A. clausi*, becomes indifferent after 30 minutes (Johnson, 1938). Experiments with *Centropages hematus*, a copepod found together with *A. tonsa*, show that it performs no migration when exposed to window light. An average of 52.1 per cent of the animals remained in the top third of the cylinders throughout the day and night (Table VI). Every field observation shows that different genera and species migrate at different times and rates. Differences between broods of the same

TABLE VI

Centropages hamatus. Average of 120 animals at 15° C. for 24 hours. Window light, July 11–12, 1941.

Time	Percentage of Animals in Top Third of Cylinders	Time	Percentage of Animals in Top Third of Cylinders
2 A.M.	56.4	2 P.M.	53.2
4	56.2	4	66.7
6	39.3	6	56.1
8	44.9	8	49.0
10	48.3	10	51.8
12 Noon	59.4	12 Midnight	44.6

Average time of sunrise, 5:16 A.M.; sunset, 8:21 P.M.

species have been found (Russell, 1928), and even between sexes of the same brood. Thus Langford (1938) finds that male *Diaptomus* moves down at the same time that the female is moving up. It is apparent that each plankton form must be investigated separately. While future investigation may show that all vertical migration is due to a single cause, it is equally probable from the data on hand that many different factors are responsible.

It is hoped to continue these experiments with other species of plankton. Isolated observation of the effect of various factors on behavior has no necessary relation to conditions in the field. If vertical migration is first reproduced in the laboratory, one can be reasonably sure that field conditions are being represented. Only then should various factors be altered in order to find the controlling ones.

SUMMARY

1. The natural diurnal vertical migration of the copepod *Acartia tonsa* can be reproduced in the laboratory. Animals kept in tall glass cylinders exposed to window light move up at night and down during the day.

2. Incandescent or fluorescent lights can be substituted for daylight without affecting this behavior, provided that the illumination is oblique to the axis of the cylinders. Migration does not depend upon the area of the source, spectral energy distribution, or total intensity of the light.

3. When illuminated obliquely to the axis of the cylinder, *A. tonsa* sinks downward. This behavior, which is followed by an upward movement in darkness, is believed to account for the normal migration of this form.

4. When the illumination is parallel to the axis of either a vertical or a horizontal tube, *A. tonsa* swims toward the light. Such highly directional illumination is not likely to be encountered in nature, and this behavior is believed to be a laboratory artifact.

5. Observation of individuals shows that the migration consists of a general trend of scattered movements. No difference was found between the sexes.

6. No evidence was found for a diurnal rhythm other than that caused by the normal alternation of day and night. Migration ceases under constant conditions; it can be reversed by illuminating the animals at night and keeping them in the dark by day; and the normal 24-hour behavior can be compressed into four hours.

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